NATIONAL ACADEMY OF SCIENCES

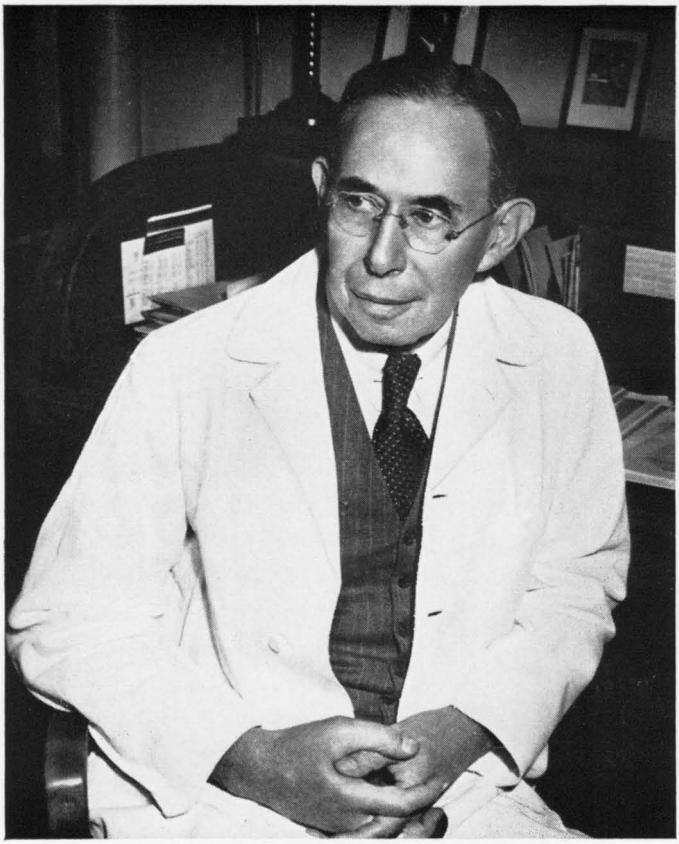
JOSEPH ERLANGER

1874—1965

A Biographical Memoir by

HALLOWELL DAVIS

Biographical Memoir



Joseph Erlanger

JOSEPH ERLANGER

January 5, 1874–December 5, 1965

BY HALLOWELL DAVIS

JOSEPH ERLANGER, Nobel Laureate with Herbert Gasser in 1944, will best be remembered for the epoch-making introduction into neurophysiology of the cathode ray oscilloscope and the exploration of the electrical activity of nerve fibers. But Joseph Erlanger was also one of the great founders of American physiology in the first quarter of the twentieth century. His stature was already established in cardiac and circulatory physiology before he turned his attention and talents to the electrophysiology of nerves. By then he had already founded the Departments of Physiology at the University of Wisconsin and at Washington University in St. Louis.

In his autobiographical reminiscences in the *Annual Review of Physiology* in 1964, he noted that his eminent career was "fraught with a series of fortunate circumstances and fortunate decisions," but with characteristic modesty he did not mention his rare technical skill as an experimenter, his great ability as a teacher, as organizer, and as a quiet but forceful leader of men, or his mastery of the almost forgotten art of frugality—of accomplishing so much with limited technical support and resources. He was truly one of the pioneers of biological science in America, and he displayed magnificently the spirit and the strength of a pioneer. Few, even among his many admirers, are aware how this spirit of self-reliance and

independence expressed itself equally in the physiological laboratory, in his independent political and religious point of view, and in his love of nature in the mountains of California and Colorado.

BACKGROUND AND BOYHOOD

Joseph Erlanger's origin was humble, with no running start toward academic eminence. Both of his parents were immigrants and neither had more than an elementary education. His father, Herman, born in Buchau am Feder See, in Württemberg, landed in New York without means in 1848. He made his way to New Orleans and thence by boat to Panama and on muleback across the Isthmus, and he finally arrived by boat in San Francisco in 1849. After unsuccessful attempts at placer mining, he settled in San Francisco, and became a merchant of moderate means. He married Sarah Galinger, the sister of his business partner. Joseph, born in San Francisco on January 5, 1874, was the sixth of their seven children, and he was the only one to complete a college education.

Thus, Joseph was the son of Californian pioneers. His boyhood was spent in the new and growing city of San Francisco. He knew and loved the outdoors and he developed an early interest in nature, particularly in the mountains and forests and in animals and how they lived and grew. His curiosity led him to examine and dissect both insects and plants. Here were the roots of his ambition to study medicine and his lifelong devotion to medical science and also of his lifelong hobby of camping and tramping in the mountains. He, in his turn, became a pioneer, not in gold mining but in medical teaching and in physiological research.

EDUCATION AND EARLY SCIENTIFIC CAREER

Erlanger himself, in his reminiscences already cited, has given us an account of his education and early career and his

associations with his colleagues. The direct, simple style, mincing no words even when speaking of misfortune and death, and thoroughly objective and modest with regard to himself, is characteristic of his writing and of his attitudes throughout his life. He tells of his early schooling at the San Francisco Boys' High School where he took the three-year "classical" course. Early he formed the ambition to study medicine. His older sister nicknamed him "Doc" because of his interest in animals and plants. In 1891 he was accepted, without examination, by the University of California at the completion of only two years of the high school course, on the basis of his scholastic standing with only a condition in Latin. In the University, he enrolled in the "College of Chemistry" as a preparation for medicine. He does not tell us how high he stood in his class. A little-known sidelight on young Joseph Erlanger is that, although he did not engage in organized sports, he did take boxing lessons from the famous champion, Jim Corbett! His family relate that he had a "terrible temper" but that early in life he learned to control it. In later years he watched boxing on TV regularly every Wednesday night. These revelations may surprise some of those who knew him as a very restrained, soft-spoken teacher and scientist.

Erlanger had planned to enter the Cooper Medical School in San Francisco, but at the suggestion of a friend, Herbert Moffitt, he applied to the newly organized Johns Hopkins Medical School. He became a member of the third class to be admitted to that institution, and he received his medical degree from it in 1899 as the second-ranking member of his class.

As a medical student he had, during a summer vacation, engaged in research under Lewellys Barker on the locus of the anterior horn cells in the spinal cord that innervate a particular muscle. The results were not published separately but were incorporated by Barker, with due credit, in his volume *The Nervous System and Its Constituent Neurons.* A second re-

search, in association with a fellow student, Walter Hewlett, dealt with the digestion and absorption of food in dogs with shortened intestines.

After a year of internship under Sir William Osler at the Johns Hopkins Hospital, Erlanger, influenced no doubt by his laboratory experiences, made his choice for a career as teacher and investigator rather than as a practicing physician. He was granted a coveted fellowship in pathology in William H. Welch's department, but resigned it at the last moment when he was offered an assistantship in physiology by William H. Howell. He knew that physiology was more to his liking.

THE YOUNG PHYSIOLOGIST

Erlanger taught at the Hopkins Medical School until 1906. His first lectures, given in 1902, dealt with digestion and metabolism. In the student laboratories he used to good advantage his deftness of hand, his ingenuity, and an intuitive understanding of physical principles. One episode is legendary. During the preparation for a demonstration to the medical students of a delicate and newly-imported blood-pressure machine, the Mosso sphygmomanometer, the glass instrument was smashed beyond repair. (Erlanger writes simply, "I broke it.") However, he immediately improvised a larger and more rugged substitute which measured and recorded the pulsation of the upper arm instead of the first fingers of the two hands. It worked. Later Erlanger described the instrument and it was manufactured by a New York firm. The present writer remembers this instrument lovingly from his use of it as a medical student and, in his turn, as a laboratory instructor in physiology. Actually, the Erlanger model was superseded in general use by the German instrument of von Recklinghausen which, according to Erlanger, "used the same principle but was of superior construction."

In the laboratory Erlanger used his sphygmomanometer in a study, with Donald R. Hooker, of the relation of blood flow to orthostatic albuminuria. A major generalization, set forth in their 233-page monograph, was that the output of albumin depended primarily on the pulse pressure, not on the mean blood pressure. Another important study during this period concerned the transmission of excitation from the auricle to the ventricle of the dog's heart. Reliable conduction with an appropriate delay is required for an effective coordinated beat. Failure is known as "heart block." Opinion varied as to whether the conduction depended exclusively on the narrow specialized atrioventricular "bundle of His," as to whether regeneration following injury was possible, and as to whether other tissue might perform the function vicariously. Erlanger followed carefully a clinical case of Stokes-Adams syndrome (slow pulse and fainting spells) with complete heart block. The heart block was gradually relieved during successful antisyphilitic treatment. Erlanger reproduced the sequence in dogs, first in acute and later, after he moved to Madison, in chronic experiments by carefully graded injury to the bundle of His. The cardiac surgery and the use of graded pressure, applied by a special clamp of Erlanger's design, represent technical achievements of a high order. These and related experiments firmly established the complete and permanent dependence of auriculoventricular conduction on the bundle of His.

A still later phase of these cardiac studies served to establish the locus of the origin of the cardiac impulse in normal and abnormal conditions. Erlanger was not alone in this work but he made major experimental contributions and his point of view relating the problem to the phylogenetic and embryonic development of the heart served to clarify confusing observations. His Harvey Lecture of 1912 entitled "The Localization of Impulse Initiation and Conduction in the Heart" had a pro-

found influence on the thinking of both physiologists and cardiologists.

During and for a time after World War I, problems of blood pressure and wound shock dominated cardiac physiology in the United States. Erlanger undertook studies of these problems and became interested in the arterial sounds of Korotkoff that occur during partial compression of the artery and are routinely employed in determining arterial pressure in man. Erlanger analyzed the production of these sounds in experiments on dogs in which the exposed femoral artery was compressed in a special air-tight chamber under visual observation and with correlated mechanical records and auditory detection of the sounds. The first sound to appear, as the compressing pressure falls slowly, is about 3 mm Hg below the systolic pressure, i.e., the pressure at which the blood first penetrates through the compressed artery. The transition from a sharp to a dull sound, not the cessation of all sound, correctly signals the diastolic pressure. Actually the cessation of sound is still often employed clinically to determine the diastolic pressure. Erlanger commented briefly in 1964, "For routine purposes it may be good enough, but actually it is lower than the diastolic pressure."

All of these studies of the heart and circulation established Erlanger as one of the leading physiologists in this country long before he began the researches in neurophysiology for which he was awarded the Nobel Prize.

THE UNIVERSITY OF WISCONSIN AND WASHINGTON UNIVERSITY

The story of the first phase of Erlanger's career as an investigator has outrun the story of his life and his development as a teacher.

During his sixth year as a physiologist at the Hopkins Medical School (1906), Erlanger accepted the appointment as Professor of Physiology and Physiological Chemistry in the medical school that was being started in Madison by the University of Wisconsin. (His salary at Baltimore had been $1500 a year. At Madison it was increased to $3000.) At Madison, Erlanger became a pioneer in organizing and equipping a department and laboratories for his two subjects. The space available was the attic and second floor of the old Chemical Engineering building. Two years were devoted to establishing laboratories and to developing a complete set of lectures, in manuscript form, covering the entire field of medical physiology. These manuscripts, updated year by year, he used throughout his teaching career. His lectures were famed for their clarity and organization, and they were completely devoid of byplay or attempts at humor!

Erlanger remained at Madison for only four years. In 1910 he was persuaded to pioneer once more and became one of a group of new department heads at the reorganized School of Medicine of Washington University in St. Louis. That group, recruited by the Chancellor, David Houston, and the President of the Board of Trustees, Robert S. Brookings, included, in addition to Erlanger (physiology), Dock (medicine), Howland (pediatrics), Opie (pathology), Shaffer (biochemistry), and Terry (anatomy). Others were added during the next decade but these constituted the nucleus. New quarters at the present location of the school began to be used in 1914. In 1916 Erlanger brought from Madison to St. Louis Herbert S. Gasser, with whom he collaborated so successfully in the second phase of his scientific career. Erlanger not only organized the Department of Physiology, he elevated it to international prominence and ran it for thirty-five years until his retirement from teaching in 1946.

Erlanger was a strong personality, independent in his social, political, and religious views. He wore high collars long after other men had forgotten all about them. When his university sent him a personal-history questionnaire, he wrote in the space for politics the word "Mugwump" to express his disapproval of what he considered an unwarranted prying into his private life. He was a member of the Humanist Society, and to the extent that he had a religious affiliation it was Humanism. His wife and children were Unitarians. He could be outspoken when pressed on social issues. Asked, in a friendly gathering, for his views concerning the problem of the Negro in America, he replied quietly but firmly that racial intolerence will continue for generations until the color line is erased by intermarriage between the races. These were strong words in St. Louis, spoken before the days of integration.

In spite of firm convictions and a strong but carefully controlled temper, Joseph Erlanger enjoyed a singularly warm and close-knit family life and he was considered "good fun" by those who came to know his sense of humor. He never himself told an off-color story, but he was no prude and could laugh with the rest and not spoil the fun. Although he did not usually smoke, he would take a cigarette after dinner to make his guests feel at ease. In fact his social courtesy was such that once, when during a hike in the mountains he was received in a hut by the old caretaker of an unworked mine, he drank three cups of a singularly repugnant brew of "tea" rather than offend the feelings of his host.

On June 21, 1906, Joseph was married to Aimée Hirstel of San Francisco. She was a perfect wife and helpmate, who shared his love for nature and the great outdoors. She, like Joseph, was frugal, which, with a family of three children—Margaret

(b. March 1, 1908), Ruth Josephine (b. February 1, 1910, m. R. H. Swinney), and Hermann (b. April 17, 1912, d. October 14, 1959)—was a great asset with only an academic salary and no family resources in the days of World War I and later during the great depression. Aimée handled all the money, but Joseph balanced the accounts. Joseph talked only when he had something to say, not for the sake of making conversation. Aimée relieved the social situation by her easy steady flow of conversation, even although she sometimes seemed to embarrass Joseph by her unabashed adulation. But Joseph was quick to make unobtrusive but definite corrections of any misstatements of fact. Joseph and Aimée spread the warmth of their family life to include the younger members of the department. Their friendliness and Aimée's endless and excellent helpful practical advice, particularly to newcomers, were never forgotten by the recipients.

Both Joseph and Aimée were strong walkers and ardent campers. Their honeymoon was a camping trip in the Sierra Nevada Mountains of California. It nearly ended in disaster on the third day when, thanks to an incompetent guide, their pack horses, food, and equipment were all lost in a swollen river. They hiked on foot thirty miles back to civilization, and arrived exhausted, both physically and financially, but still very much in love. In spite of this misadventure, they re-outfitted themselves and continued their pack-trip for three weeks, without a guide. Later for many years they returned to the mountains of Colorado, Wyoming, or Montana habitually for six-week summer vacations as soon as the children were old enough to accompany them. Joseph no longer trusted to guides. He provided himself with excellent survey maps, backed with muslin, but scorned to carry a compass; instead he used the sun and his watch. He used his maps chiefly to identify the mountains and rivers in the landscape seen from the mountains

that they climbed. In his love for the mountains and his urge to live among them and to climb them, he showed the spirit of a pioneer.

Joseph's health was good. He was not large of stature but tough and wiry and with great endurance. He enjoyed his food and had no patience with food-and-diet fads. He always walked to work at the medical school, carrying a simple lunch in a brown paper bag. He never returned to the laboratory at night or worked on Sundays. Sunday was a family day, for playing ball or other games with his family and often other members of his department also, and with many hikes and picnics in the environs of St. Louis.

Erlanger was the last member of his department to buy an automobile. Finally, about 1922, he bought a Model T Ford with a trailer and after only six weeks of experience he drove his family in it, through Missouri mud and across Kansas, to Colorado. In 1924 he purchased a second-hand Franklin from Herbert Gasser and later, in 1929, in the same car they drove from St. Louis to Boston to attend the XIII International Congress of Physiology.

Erlanger greatly enjoyed tennis and handball, but he did not participate, even as a young man, in team games except for lacrosse at the Hopkins Medical School. He became enthusiastic and very adept at pitching horseshoes. This was a favorite sport and form of relaxation at the laboratory at lunch time or at the end of the day. Erlanger practically coerced (or shamed) his younger colleagues into pitching, whatever the weather, once even when the ground was covered with glare ice. His opponent announced, as they returned to the laboratory that noon, "The Chief slid a ringer today."

Erlanger's great hobby was the outdoors, particularly walking and hiking. His research should also be considered a hobby. Next came music. He and Aimée attended the symphony

concerts regularly until her health failed in later years. Joseph played a wooden flute and for some years participated in an informal orchestra, recruited chiefly among the medical faculty. He read the daily news regularly and the *Saturday Review* and the *New Yorker* avidly and also much biography and history. Like many careful readers, he marked freely the key passages in his books and magazines.

After retirement from teaching in 1946, Erlanger continued to go regularly to his laboratory and the library until Aimée's health and physical vigor began to fail. Then for several years, until her death, he turned completely to caring for her, with complete and unstinting devotion. He outlived her by several years, clear of mind and in good health until the time of his death in 1965.

ERLANGER THE TEACHER

Erlanger was an influential and effective teacher, both for medical students and for his graduate students. His lectures were models of clarity and logical devopment. The students dreaded his merciless Saturday morning oral quizzes, but they learned much from them. He taught meticulous attention to detail in the laboratory. His surgical skill was unusual. Even when operating on the heart of a dog in the World War I era, he wore a frock coat instead of a laboratory gown, and it is said that he never once soiled it with a drop of blood. He insisted on clear, direct, logical exposition in his own and his students' papers and theses. In only one form of communication did he have a weakness: his handwriting was atrocious. One time he even had to call on Miss Stubinger, his faithful secretary for thirty-five years, to decipher some of his numerous and devastating annotations on the draft of a graduate student's thesis.

Erlanger practiced and taught respect and kindness and good care for laboratory animals. Once an antivivisectionist, who

had heard of his cardiac operations on surviving dogs, sneaked in and opened the cages to allow the animals to escape from their supposed life of torture. The animals all ran out, but Erlanger's care and treatment of them had been so good that every one of them returned home to the laboratory at nightfall. On another occasion he strongly reprimanded a graduate student for performing arterial ligations on surviving frogs without proper consultation with him as laboratory director concerning the necessity and propriety of such drastic procedure. He taught respect for the life of a frog as well as cats and dogs.

Erlanger had only three graduate students who achieved the Ph.D. degree. They were Francis O. Schmitt, Edgar A. Blair, and Albert S. Harris, but many of his junior department members and visiting fellows have achieved eminence. Among them are Herbert Gasser, George Bishop, A. M. Monnier, Georges Coppée, Pierre Rijlandt, Joseph Hinsey, Helen Graham, Peter Heinbecker, Arthur Gilson, H. L. White, Gordon Schoepfle, Crighton Bramwell, and Geoffry Bourne. Particularly in the second phase of his experimental career, the neurophysiological era, did his influence spread widely in the Washington University Medical School and its hospitals. He established an eminence in neurology and neurophysiology that still persists as the Erlanger tradition today.

ERLANGER AND AMERICAN PHYSIOLOGY

Erlanger was elected to the American Physiological Society in 1901, only one year after embracing physiology as his career. He was elected to its Council in 1910, and with the exception of a single year, 1924, remained on the Council in one capacity or another until 1929. He was Treasurer from 1913 to 1923, and as such he helped to shape the financial policies of the Society during and following the transfer of the *American Journal of Physiology* to the Society in 1922. He accomplished the incorporation of the Society as a Missouri corporation in 1923.

He served as President in 1926-1927 and 1928 and through the XIII International Congress of Physiology at Boston in 1929. He displayed conservative leadership in the business and organizational work of the Society and he carried a large share of responsibility.

In a less formal way, Joseph Erlanger and Alexander Forbes, as the two senior electrophysiologists of their generation, exerted a profound influence on the development of neurophysiology in America. This was accomplished through the formation, during the late 1920s, of a group of neurophysiologists, orginally twelve in number, interested in the fundamental nature of the nerve impulse, the electrical excitation of tissue, and so on. This group met regularly for lunch or dinner and a discussion during each annual meeting of the American Physiological Society. They called themselves "The Axonologists." No one is quite sure when the group was organized on an informal but continuing basis, but once it had been enlarged from the original twelve and its meetings opened to all, its numbers and its influence grew rapidly. Erlanger and Forbes were the spiritual leaders, and the ideas, the methods, the techniques, and the latest results of their laboratories and others were discussed and exchanged. The cathode-ray oscilloscope was soon recognized as the only adequate means of recording the nerve action potential. A forum was provided for lively debates concerning the nature of synaptic action, whether electrical or chemical. Only after "The Axonologists" had dissolved, when the group's increased membership made impossible the former lively spontaneous discussions, did the members realize how important it had been in stimulating and shaping the development of neuro-electrophysiology.

OTHER SOCIETIES AND HONORS

Joseph Erlanger was elected to the National Academy of Sciences in 1922. He served as section vice chairman of the

American Association for the Advancement of Science. As already mentioned, he shared a Nobel Prize with Herbert Gasser in 1944. Other memberships and activities are listed below. He received honorary degrees from the universities of California, Wisconsin, Pennsylvania, and Michigan, from The Johns Hopkins University, Washington University (St. Louis), and the University of Brussels.

ERLANGER AND THE CATHODE RAY OSCILLOSCOPE: A NOBEL LAUREATE

The second phase of Erlanger's physiological research—his most famous piece of scientific pioneering—began soon after World War I. Erlanger had long been interested in the cardiac impulse, the wave of excitation which like a nerve impulse sweeps down the bundle of His, and in the excitation of cardiac tissue by electric shocks. The electrical action current associated with the impulse could be studied with fair precision by means of the Einthoven string galvanometer, but the currents were too weak and too rapid in their time course for really adequate recording and analysis, nor could the instruments portray the form of the electric shocks used as stimuli. Alexander Forbes at Harvard met the problem of weakness of the action currents by developing the condenser-coupled amplifier as an outgrowth of his wartime experience with the radio compass. He combined his amplifier with a string galvanometer, but even so the problem of the lag and the overshoot of the recording instrument due to its inertia still remained. By 1921 Gasser and Newcomer had also developed an amplifier and, with it and a string galvanometer, had studied the action potentials of the phrenic nerve. Gasser at this time learned of the cathode ray tube, or "Braun tube," made by the Western Electric Company, which made use of an inertialess stream of electrons. Such tubes in modern form are now familiar

in daily life as the TV tube and are the basis of most high-speed electronic measurements, but when the Western Electric Company in 1921 refused to sell a cathode ray tube, presumably because of possible patent infringements, Erlanger and Gasser undertook to build one of their own! A distillation flask was the tube. Erlanger wrote of it thus: "One pair of deflection plates was mounted inside and a pair of solenoid coils outside. A mechanical revolving potentiometer provided the sweep circuit."

George H. Bishop, who joined Erlanger and Gasser in 1923, spoke as follows of the next steps, at the Joseph Erlanger Memorial Service in 1966.

"These two men were not particularly sophisticated in either electronics or physics, and their troubles were various and cumulative. Noise in the amplifier, noise in the environment, vibration from trucks and sparks from the trolley line called for shielding and insulation, switches had to be devised which would operate in fractions of a thousandth of a second, without chatter, etc. Finally, no camera would photograph the dim trace obtainable at the speed required to record the nerve impulse. The first records were obtained by holding a photographic film against the end of the tube and repeating the stimuli until an accumulation of superposed traces induced a bleary line on a somewhat fogged background. I can only compare their progress to the trek of the pioneers in oxcarts across the plains and mountains of the West. They were pioneers of electrophysiology, and they encountered every conceivable obstacle but the Indians. Far more time was spent upon reconstruction of apparatus than on the recording of nerve, when one good record occasionally made a successful day.

"I have gone back and read again those early papers. The problems now look so simple, the results so elementary, the difficulties met so trivial, that one has to think in terms of an

era when electronics was at as elementary a stage as was the physiology of nerve, and as was the sophistication of the workers learning how to deal with both.

"This was the first application of the cathode ray device to biology, and one of the first at least of its applications to any specific problem. The present generation of electrophysiologists stand on the shoulders of Gasser and Erlanger."

The first major discovery made with the new instrument was the different velocities of conduction in nerve fibers of different diameter. This in turn led to the study of other properties of fibers of different sizes, with and without a myelin sheath. These distinctions and the resulting classification of nerve fibers are among the fundamentals of modern neurophysiology.

Erlanger and Gasser transported their bulky homemade equipment to Boston in 1929 and at the XIII International Congress of Physiology gave the first public demonstration of the action potentials of the slow "C" fibers.

The next quest was to relate the different classes of fiber to different functions or sense modalities, such as motor *vs.* sensory and touch *vs.* temperature *vs.* pain. This problem proved far more difficult, and actually it now seems that only the broadest correlations of function with structure and conduction velocity, such as somatic *vs.* autonomic, are possible. Nature puts together its neuronal building blocks in complicated ways; perhaps, as Bishop has suggested, the groupings of nerve fibers are more significantly related to the successive phylogenetic projections and elaborations of central functioning than to specific sensory and motor modalities.

The point is that Erlanger and Gasser's great achievement lay not so much in the particular discoveries that they made as in blazing the trail and showing the way. They were duly and properly honored for this by the award to them jointly

of the Nobel Prize for Physiology and Medicine in 1944.

Erlanger and Gasser have told their story, not only at the time of receiving the Nobel award in Stockholm, but in a series of lectures they delivered at the University of Pennsylvania and published as a book entitled *Electrical Signs of Nervous Activity*. In it each of them tells his own part of the story, divided naturally according to their individual interests. Characteristically, they did not always share the same interpretation of their own observations. Equally, they respected one another's views and each held to his own in friendly disagreement. In the preface of the book they report how and where they planned the lectures. It was on a holiday in Colorado in 934, and "as we sat upon a ledge high up in the Rocky Mountains . . . viewing the panorama of lofty peaks spread out before us, our conversation turned to problems of nerve physiology."

CHRONOLOGY

1874	Born January 5, San Francisco
1891	Admitted to University of California after two years of high school
1895	B.S., University of California
1899	M.D., Johns Hopkins Medical School
1899-1900	Resident Medical Officer, Johns Hopkins Hospital
1900-1903	Assistant and Instructor in Physiology, Johns Hopkins Medical School
1903-1904	Associate in Physiology
1904-1906	Associate Professor in Physiology
1906	Married June 21 to Aimée Hirstel, San Francisco
1906-1910	Professor and Head of Departments of Physiology and Physical Chemistry, University of Wisconsin
1910-1946	Professor and Head of Department of Physiology, Washington University (St. Louis)
1912	Harvey Lecture (New York): "The Localization of Impulse Initiation and Conduction in the Heart"
1922	First publication of use of cathode ray oscilloscope
1926-1929	President of American Physiological Society
1928	Harvey Lecture (New York): "Analysis of the Action Potential in Nerve"
1929	Demonstration of nerve impulses in "C" fibers at XIII International Congress of Physiology (Boston)
1930	Hitchcock Lecturer, University of California
1936	Eldridge Reeves Johnson Lectures (Philadelphia): "Electrical Signs of Nervous Activity" (with H. S. Gasser)
1944	Awarded Nobel Prize in Physiology and Medicine (with H. S. Gasser)
1946	Emeritus Professor of Physiology, Washington University School of Medicine
1947	Presentation of Nobel Prize, December 10, in Stockholm
1965	Died December 5 in St. Louis

HONORS AND DISTINCTIONS

HONORARY DEGREES

1932	LL.D., University of California
1936	Sc.D., University of Wisconsin
1936	Sc.D., University of Pennsylvania
1937	Sc.D., University of Michigan
1946	Sc.D., Washington University
1947	LL.D., The Johns Hopkins University
1948	Hon. D., Free University of Brussels

MEMBERSHIPS

National Academy of Sciences
American Philosophical Society
American Physiological Society

1901	Member
1910-1912	Councilor
1913-1923	Treasurer
1926-1929	President

American Medical Association
American Association for Advancement of Science
Society of Experimental Biology and Medicine
Association of American Physicians
Deutsche Acad. Naturforscher (Halle)
Societé Philomatique (Paris)
Alpha Omega Alpha
Sigma Xi

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KEY TO ABBREVIATIONS

Am. Heart J. = American Heart Journal
Am. J. Physiol. = American Journal of Physiology
Arch. Internal Med. =Archives of Internal Medicine
Bull. St. Louis Med. Soc. = Bulletin of the St. Louis Medical Society
J. Am. Med. Assoc. = Journal of the American Medical Association
J. Exp. Med. = Journal of Experimental Medicine
J. Neurophysiol. = Journal of Neurophysiology
Johns Hopkins Hosp. Bull. = Johns Hopkins Hospital Bulletin
Johns Hopkins Hosp. Rept. = Johns Hopkins Hospital Reports
Proc. Soc. Exp. Biol. Med. = Proceedings of the Society for Experimental Biology and Medicine
Wisconsin Med. J. = Wisconsin Medical Journal
Zentr. Physiol. = Zentralblatt für Physiologie

1901

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